

# Development and characterization of two new *Triticum aestivum–Dasypyrum villosum* Robertsonian translocation lines T1DS·1V#3L and T1DL·1V#3S and their effect on grain quality

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**Abstract** *Dasypyrum villosum* (L.) Candargy is a diploid, wild relative of bread wheat (*Triticum aestivum* L.). Previous studies showed that *D. villosum* chromosome 1V has genes that encode seed storage proteins that may be used to enhance the grain quality of bread wheat. As a first step in genetic transfer, the present study was initiated to develop compensating Robertsonian translocations involving wheat chromosome 1D and *D. villosum* chromosome 1V and to analyze their effects on grain quality. A monosomic 1D stock was crossed with the disomic addition stock DAI1V#3 and the double monosomic plants (20" + 1D' + 1V#3') were self pollinated. Two co-dominant STS markers (BE499250 and BE591682) polymorphic for the short arm of 1V#3S and two dominant STS markers (BE518358 and BE585781) polymorphic for the long arm of 1V#3L were developed to screen a large number of progeny to identify plants that had

only the 1V#3S or 1V#3L arms. Five compensating Robertsonian heterozygous translocations, two (plants #56 and #83) for the short arm (T1DL·1V#3S) and three (plants #7, #123, and #208) for the long arm (T1DS·1V#3L) were identified from 282 F<sub>2</sub> plants and confirmed by genomic in situ hybridization and C-banding analyses. Two homozygous translocations T1DL·1V#3S (plants #14 and #39) were identified from 52 F<sub>3</sub> plants derived from F<sub>2</sub> plant #83. Four homozygous translocations T1DS·1V#3L (plants #3, #22, #29, and #30) were identified from 68 F<sub>3</sub> plants derived from F<sub>2</sub> plant #208. The homozygous translocation T1DL·1V#3S had a significantly higher (37.4 ml) and T1DS·1V#3L had significantly lower (10 ml) Zeleny sedimentation values compared to Chinese Spring wheat (30.7 ml). Our results showed that 1V#3S increased gluten strength and enhanced wheat quality, but 1V#3L decreased gluten strength and did not enhance wheat quality.

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## Introduction

Wild relatives of common or bread wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBD) are an important source of disease and pest resistance genes that can be employed in wheat improvement. *Dasypyrum*

*villosum* (L.) Candargy (syn. *Haynaldia villosa* (L.) Schur.) is an allogamous annual diploid relative ( $2n = 2x = 14$ , VV) native to the northeastern part of the Mediterranean region. Sears (1953), Hyde (1953) and Liu et al. (1988) produced sets of wheat-*D. villosum* chromosome addition lines, but Sears's set lacked DA3V#1 and Liu et al.'s set lacked DA1V#2. Recently, Lukaszewski (unpublished data) produced a complete set of wheat-*D. villosum* chromosome addition lines designated DA1V#3 to DA7V#3.

*D. villosum* has many agronomically important traits, including resistance to leaf rust, stem rust, and stripe rust (Hyde 1953; Chen et al. 2001, 2002), powdery mildew (Qi et al. 1993; Chen et al. 1995, 1997; Li et al. 2005), take-all (Linde-Laursen et al. 1973), eyespot (Murray et al. 1994), and spindle streak mosaic viruses (Zhang et al. 2005) as well as winter hardiness, vigorous tillering ability, multi-spikelets, high grain protein content, and salt and drought tolerance (Blanco et al. 1983). However, when using alien genes from the tertiary gene pool in wheat improvement, the alien target gene needs to be in the form of a cytologically stable, compensating wheat-alien whole-arm (Robertsonian) translocation (Qi et al. 1993). Chen et al. (1995, 2002) identified a compensating T6AL·6V#2S wheat-*D. villosum* Robertsonian translocation conferring resistance to powdery mildew (*Pm21*) and wheat curl mite colonization. Zhang et al. (2005) developed a compensating T4DL·4V#2S translocation stock, that was resistant (*Wss1*) to wheat spindle streak mosaic virus.

Chromosome 1V has genes encoding high-molecular-weight glutenins (*Glu-V1*) that are orthologous to the *Glu-A1*, *Glu-B1* and *Glu-D1* loci of hexaploid wheat (Blanco et al. 1991; Montebello et al. 1987). Zhong and Qualset (1993) identified 14 alleles for *Glu-V1* coding for null, single and two HMW-protein subunits. Chromosome 1V also encodes for most of the prolamin genes, sulfur-poor ( $\omega$ -type) and sulfur-rich ( $\gamma$ -type) monomeric units (*Gli-V1*) that are orthologous to the *Gli-1* loci of wheat, and the low-molecular-weight (LMW) polymeric prolamin proteins (*Glu-V3*) (Blanco et al. 1991; Shewry et al. 1987). In the present study, we used molecular markers and genomic in situ hybridization (GISH) to develop and characterize two new compensating T1DL·1V#3S and T1DS·1V#3L Robertsonian translocation stocks and evaluated their effects on wheat grain quality.

## Materials and methods

### Plant material

The plant material consisted of the *D. villosum* accession TA10220; the disomic chromosome addition line DA1V#3 kindly provided by Dr. A. J. Lukaszewski, University of California, Riverside; the bread wheat cultivar 'Chinese Spring (CS)' and the derived nullisomic/tetrasomic (NT, N1AT1D, N1BT1D, N1AT1B), and ditelosomic (Dt, Dt1AS, Dt1AL, Dt1BS, Dt1BL, Dt1DS, and Dt1DL) stocks. All stocks are maintained by the Wheat Genetic and Genomic Resources Center at Kansas State University. The monosomic stock M1D was crossed as female with DA1V#3, and the progeny was screened for plants that had  $2n = 42$  chromosomes and were double monosomic for chromosomes 1D of wheat and 1V#3 of *D. villosum* (20" + 1D' + 1V'). These plants were self-pollinated and their progenies screened by molecular markers to identify putative Robertsonian translocations, which were then verified by GISH.

### Molecular marker development

Leaf samples were collected at the 2–3-leaf stage, and genomic DNA was isolated according to Qi et al. (2003). We developed STS (sequence target site) markers for screening large numbers of progeny for the presence of putative 1V–1D Robertsonian translocations. Forty-eight, bin-mapped ESTs (expressed sequence tags) for each group-1 chromosome arm were selected from the wheat EST mapping project (<http://wheat.pw.usda.gov/NSF/data.html>), including 24 markers from the centromeric bin and 24 markers from the telomeric bin. The sequences of these 96 ESTs (<http://www.ncbi.nlm.nih.gov/Genbank/>) were used to design EST-specific primers using the software Primer 3 (<http://frodo.wi.mit.edu>). The PCR protocol followed that of Qi et al. (2007). For obtaining higher levels of polymorphism, the PCR products were digested with the 4-base cutter enzymes *Alu*I, *Hae*III, *Msp*I and *Rsa*I.

### Cytogenetic analysis

C-banding and chromosome identification were according to Gill et al. (1991) and Friebe et al. (1987). The procedures for GISH followed Qi et al.

(2008). Genomic DNA of *D. villosum* labeled with FITC-12-dUTP was used as a probe. Slides were analyzed with an epifluorescence Zeiss Axioplan 2 microscope. Images were captured using a SPOT 2.1 CCD (charge-coupled device) camera (Diagnostic Instruments; <http://www.diaginc.com>) and processed with Photoshop v5.5 software (Adobe Systems; <http://www.adobe.com>).

#### Evaluation of grain quality

The T1DS·1V#3L and T1DL·1V#3S stocks were planted in the field at Yangling, Shaanxi, China, during the 2008–2009 growing season in a randomized plot design. Each plot with three replications had two 2 m rows with 0.25 m spacing between rows and 0.1 m between plants within the rows. At planting, 300 kg N and 240 kg P<sub>2</sub>O<sub>5</sub> were applied per hectare. Field management followed local practices. Grain protein content was calculated as  $5.7 \times$  the nitrogen concentration determined by the micro-Kjeldahl method (De Pace et al. 2001). Zeleny sedimentation tests were performed according to the AACC (1995) method 56-61A (Li et al. 2007). Analysis of variance was performed on original data for grain protein content and Zeleny sedimentation values using the Tukey's HSD procedure and DPS<sup>TM</sup>v11.50 software designed by Hangzhou Refine Information Tech. Co. LtD of Zhejiang University (<http://www.chinadps.net>).

## Results

### Marker development

Twenty-four EST-primers from the distal region and 24 EST-primers from the proximal region of each arm

of the wheat group-1 chromosomes were used to screen CS and the disomic addition line DA1V#3. The PCR products were separated on 1% agarose gels. Only primer BE499250 from the proximal region of chromosome 1S amplified a polymorphic band in DA1V#3. In order to increase the level of polymorphism, the PCR products were digested with the 4-base cutter restriction enzymes *Alu*I, *Hae*III, *Msp*I and *Rsa*I before separation of PCR products on 1% agarose gels. Three additional primers detected polymorphisms between CS and DA1V#3. Of the polymorphic markers, BE591682 was derived from the distal region of 1S, BE518358 was derived from the proximal region of 1L and BE585781 is derived from the distal region of 1L. Therefore, the four EST-STS loci covered the short and long arms of group-1 chromosomes. The primer/enzyme combinations are listed in Table 1. Nullisomic-tetrasomic and ditelosomic stocks of group-1 chromosomes were used to map and identify 1DS- and 1DL-specific fragments. Of the four polymorphic STS markers, the two short arm markers were co-dominant. The 1DS fragments detected by these two markers can be distinguished from those of chromosomes 1A and 1B (Fig. 1). The other two EST-STS loci located on 1L were dominant markers as the 1DL band co-migrated with those of 1A and 1B, but 1V#3L was polymorphic (Fig. 2).

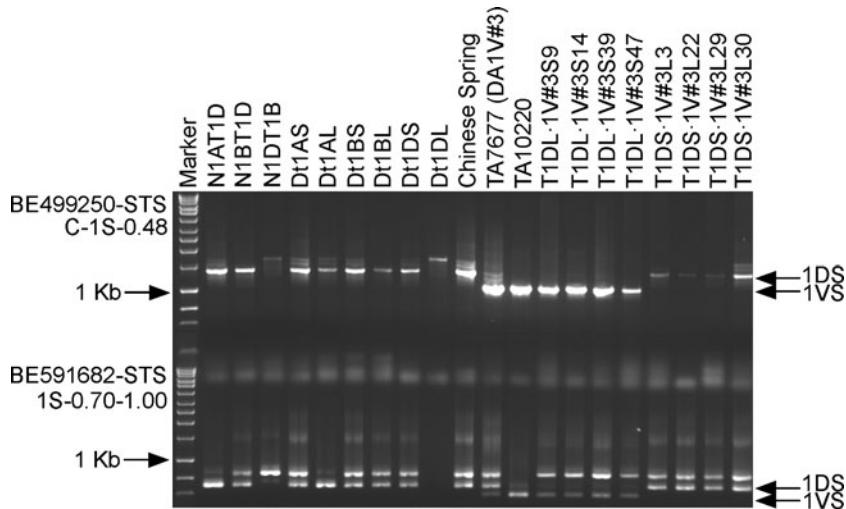
### Identification of homozygous compensating Robertsonian translocations

A total of 282 F<sub>2</sub> plants derived from a double monosomic F<sub>1</sub> plant with 2n = 42 were screened with the four STS markers. Thirty-six plants showed polymorphic bands only for the two short-arm markers, whereas 27 plants showed polymorphic bands only for the two long-arm markers.

**Table 1** Primer sequences of STS markers derived from wheat ESTs on group 1 chromosomes and primer/enzyme combinations producing polymorphic PCR products

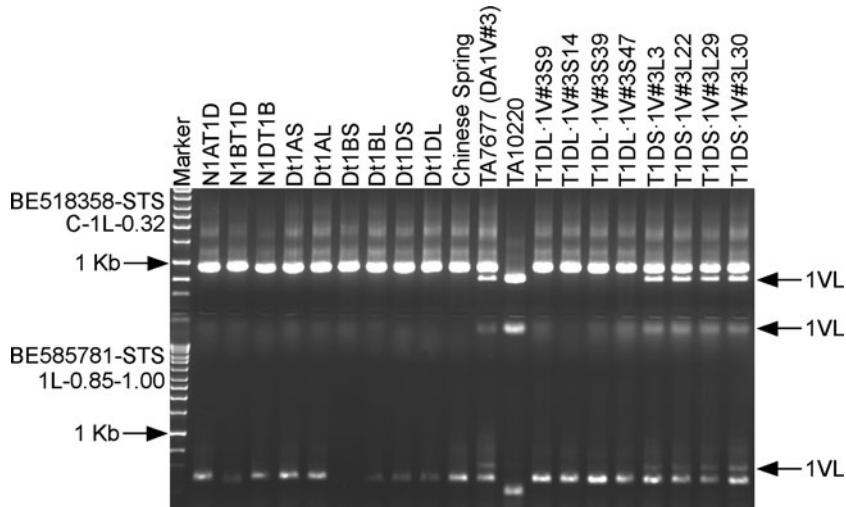
Marker	EST	Location of deletion bin <sup>a</sup>	Forward primer 5'-3'	Reverse primer 5'-3'	Enzyme
BE591682-STS	BE591682	1S-0.70-1.00	TGTTTGGGTGTTCACTCA	AGCAATTGGATGACGAACC	<i>Rsa</i> I
BE499250-STS	BE499250	C-1S-0.48	TGTTCAAGAGGTGCTCATCG	ATTGCACGGTACCTCTCCCTG	
BE518358-STS	BE518358	C-1L-0.32	TGTCTCTGTTGGGCCTCTT	TGCACTTGCTGAGTCCATT	<i>Hae</i> III
BE585781-STS	BE585781	1L-0.85-1.00	CGATGAGATCGCTGTGAAGA	GTGTCTGGTCTCTCCGAAA	<i>Rsa</i> I

<sup>a</sup> Chromosome bin locations in group-1 chromosomes of wheat ESTs was referenced to [http://wheat.pw.usda.gov/cgi-bin/westsql/map\\_locus.cgi](http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi) and was indicated by the consensus bins for group 1 chromosomes



**Fig. 1** PCR pattern of BE499250-STS and BE591682-STS markers tested with nullisomic-tetrasomic (NT) and ditelosomic (Dt) stocks of group-1 chromosomes and wheat-*D. villosum* translocations. The 1DS fragments amplified by BE499250 and BE591682 primers can be distinguished from

1A and 1B. The 1DS fragment was absent in N1DT1B, Dt1DL, the *D. villosum* accession line TA10220, and all four T1DL·1V#3S plants. A 1VS-specific fragment was detected in TA7677 (DA1V#3), TA10220 (*D. villosum*) and all four T1DL·1V#3S translocations

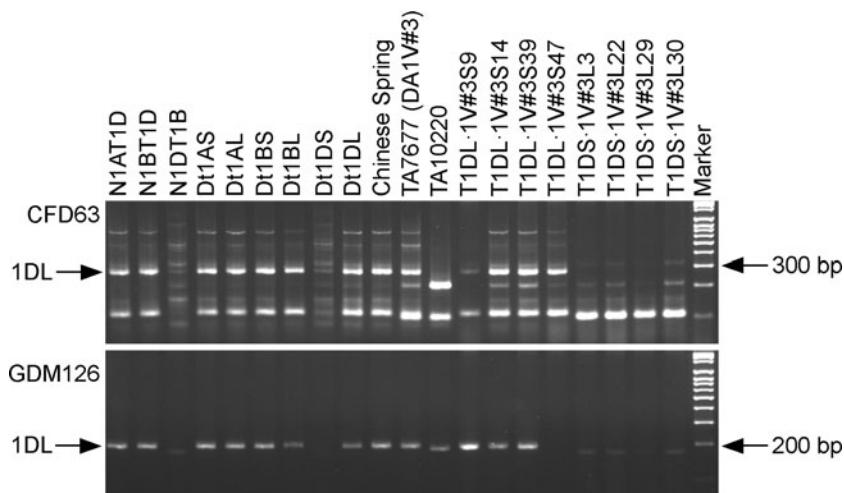


**Fig. 2** PCR pattern of BE518358-STS and BE585781-STS markers tested with nullisomic-tetrasomic (NT) and ditelosomic (Dt) lines of group 1 and wheat-*D. villosum* translocations. The 1DL fragment cannot be distinguished from 1A and 1B. The 1VL-specific fragments amplified by the two EST

primers were present in TA7677, TA10220 and all four T1DS·1V#3L translocations. The primer BE585781 amplified a 1VL polymorphic fragment in TA10220 that is different from DA1V#3. This can be explained by heterogeneity of open-pollinated *D. villosum*

Five compensating, heterozygous, Robertsonian translocation plants, one noncompensating, heterozygous, Robertsonian translocation plant and one plant with a wheat-1V#3 recombinant chromosome were identified by GISH analysis. Three of the compensating

Robertsonian translocations involved 1V#3L (plants #7, #123 and #208) and two involved 1V#3S (plants #56 and #83). C-banding analysis identified the translocation chromosomes as T1DS·1V#3L and T1DL·1V#3S (Fig. 4).



**Fig. 3** PCR pattern of SSR markers CFD63 and GDM126 mapped on 1DL with nullisomic-tetrasomic (NT) and ditelosomic (Dt) lines of group-1 and wheat-*D. villosum* translocations. The 1DL-specific fragments amplified by CFD63 and GDM126 were absent in N1DT1B, Dt1DS and all four

T1DS-1V#3L lines, but were present in the T1DL-1V#3S14 and T1DL-1V#3S39 lines. T1DL-1V#3S9 had the GDM126 fragment, but lacked the CFD63 fragment; T1DL-1V#3S47 had the CFD63 fragment, but lacked the GDM126 fragment, indicating that the 1DL arms in the two lines have deletions

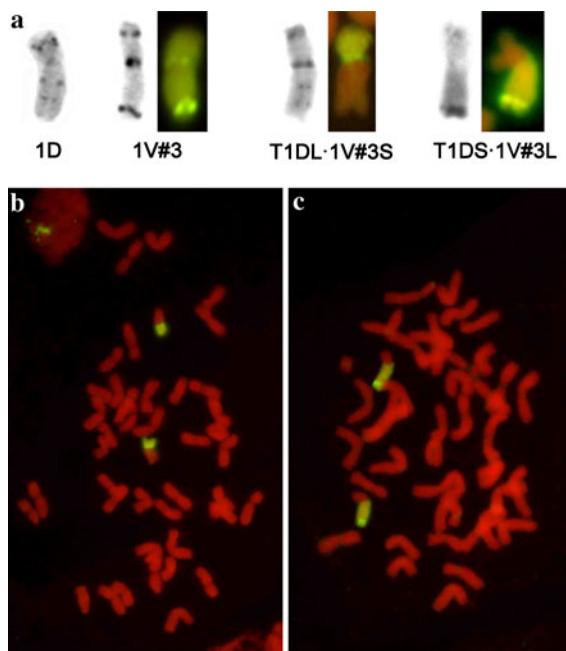
Fifty-two F<sub>3</sub> plants derived from F<sub>2</sub> plant #83 that was heterozygous for the T1DL-1V#3S translocation were screened with the four STS markers used to screen the F<sub>2</sub> population. The two co-dominant markers BE499250-STS and BE591682-STS also can be used to detect the 1DS arm (Fig. 1). We used the SSR markers GDM126 and CFD63, mapped on 1DL, to identify 1DL (Fig. 3). Twenty-seven plants showed polymorphic fragments for the two short-arm markers BE499250-STS and BE591682-STS, but there was no plant polymorphic for the two long-arm markers. Of the 27 1V#3S F<sub>3</sub> plants, two (#14 and #39) were homozygous for translocation T1DL-1V#3S; both had the 1DL-specific fragments, but were missing the 1DS fragment (Figs. 1, 3). GISH further confirmed that they were homozygous translocations with 2n = 42 and were designated as TA5615 (Fig. 4). The 1DS-specific fragments were also absent in plants #9 and #47 with 1V#3S, but plant #9 lacked the 1DL-specific fragment detected by SSR marker CFD63. Plant #47 lacked the 1DL-specific fragment detected by SSR marker GDM126, indicating that the 1DL chromosome arms in plants #9 and #47 had deletions.

Similarly, 68 F<sub>3</sub> plants derived from F<sub>2</sub> plant #208 heterozygous for the T1DS-1V#3L translocation were screened with four STS markers and two 1DL SSR

markers. Twenty-four plants showed polymorphic fragments for the two long-arm markers BE518358-STS and BE585781-STS. No plant polymorphic for the two short arm markers was identified. Of the 24 polymorphic 1V#3L F<sub>3</sub> plants, four (#3, #22, #29 and #30) were homozygous for T1DS-1V#3L based on the presence of 1DS-specific fragments and absence 1DL-specific fragments (Figs. 1, 2, 3, 4). The homozygous T1DS-1V#3L translocation stock was designated as TA5616.

#### Grain quality evaluation

The seed protein concentration of Chinese Spring and the translocation stocks T1DS-1V#3L and T1DL-1V#3S were 15.47, 15.20 and 14.81%, respectively, which were not significantly different. The Zeleny sedimentation value of T1DL-1V#3S was 37.4 ml, which is significantly higher than that of CS (30.7 ml), whereas the translocation line T1DS-1V#3L had a significantly lower Zeleny sedimentation value (10.0 ml) compared to CS (Table 2). Because the Zeleny sedimentation value is an indicator of end-use quality and a good predictor of gluten strength, our results suggest that 1V#3S can increase gluten strength and enhance wheat quality, whereas 1V#3L may decrease gluten strength.



**Fig. 4** C-banding and GISH patterns of wheat-*D. villosum* compensating Robertsonian translocation stocks. **a** C-banding and GISH patterns of the critical chromosomes: from left to right, wheat chromosome 1D, *D. villosum* chromosome 1V, wheat-*D. villosum* Robertsonian translocation chromosome T1DL·1V#3S and T1DS·1V#3L; **b** GISH pattern of a plant homozygous for T1DL·1V#3S; **c** GISH pattern of a plant homozygous for T1DS·1V#3L

## Discussion

The objective of this study was to produce genetically compensating Robertsonian translocations between wheat chromosome 1D and *D. villosum* chromosome 1V. To transfer whole alien chromosome arms to wheat, the centric breakage-fusion behavior of univalents can be exploited (Sears 1952). The alien chromosome and a homoeologous wheat chromosome are isolated in monosomic condition. In such double monosomic plants, both monosomes stay univalent at

meiotic metaphase I. The two univalents have a tendency to break at the centromeres, followed by fusion of the broken arms, giving rise to Robertsonian whole-arm translocations (Robertson 1916). In the present study, five compensating Robertsonian translocations were identified among 280 F<sub>2</sub> plants (1.8%) derived from a double monosomic F<sub>1</sub> plant with 42 chromosomes. Depending on the chromosomes involved and the environmental conditions, the desired compensating wheat-alien Robertsonian translocations can be recovered at fairly high frequencies, ranging from low to almost 20% (Davies et al. 1985; Lukaszewski 1993, 1994, 1997; Friebe et al. 2005).

It is important to develop reliable and informative molecular markers to expedite the screening of large numbers of progeny for Robertsonian translocations. To ensure that the markers provide a complete coverage of the arm, one centromeric and one telomeric bin marker were developed for the short and long arm of chromosome 1V#3. From screening of 96 EST primers, two co-dominant markers (BE499250-STS and BE591682-STS) from wheat group 1S were identified that were polymorphic for 1V#3S, and two dominant markers (BE518358-STS and BE585781-STS) from wheat group 1L were polymorphic for 1V#3L. These four markers were first used to screen a large F<sub>2</sub> population from double monosomic plants for identifying plants with only 1V#3S or 1V#3L. The selected plants were further analyzed by C-banding and GISH to determine their chromosome constitutions. Two co-dominant markers for 1V#3S also distinguished 1DS-specific fragments from 1BS and 1AS and could be directly used for the selection of homozygous T1DL·1V#3S translocation plants. The combination of wheat 1DL-specific SSR markers and 1V#3L-specific markers could be used to distinguish T1DS·1V#3L homozygotes from heterozygotes. In most of the selected polymorphic plants, the short or long arms of 1V#3 were present as telosomes.

**Table 2** Mean value, standard deviation and Tukey test of significance of mean differences ( $P = 0.05$ ) for seed protein content (%) and Zeleny sedimentation value (ml) in Chinese Spring, T1DL·1V#3S and T1DS·1V#3L lines

Genotype	Seed protein content (%)			Zeleny sedimentation value (ml)		
	Mean	SD	Tukey test	Mean	SD	Tukey test
Chinese Spring (CS)	15.47	0.09	a	30.7	0.61	b
T1DS·1V#3L (TA5616)	15.20	0.13	a	10.0	0.40	c
T1DL·1V#3S (TA5615)	14.81	0.22	a	37.4	0.59	a

De Pace et al. (2001) reported that all wheat genetic stocks containing the *D. villosum* chromosome 1V had significantly higher seed protein concentrations (ranging from 13.9 to 16.7%) and SDS-sedimentation values (ranging from 99 to 131 mm) compared to 12.0% protein and a 33 mm SDS-sedimentation value for Chinese Spring wheat. The positive effects of chromosome 1V on grain quality are believed to be caused by alleles at the *Glu-V1*, *Gli-V1* and *Glu-V3* loci on chromosome 1V. In the present study, the grain protein concentrations of the translocation stocks T1DS·1V#3L and T1DL·1V#3S were similar to those of Chinese Spring. However, the translocation stock T1DL·1V#3S had a significantly higher Zeleny sedimentation value compared to that of Chinese Spring, whereas the Zeleny sedimentation value of the T1DS·1V#3L stock was lower than that of Chinese Spring. Our data suggest that the T1DL·1V#3S translocation stock may have potential in wheat improvement, and we are presently transferring this translocation into advanced breeding lines. Small seed samples of both translocation stocks are available upon request.

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